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A ROLE FOR WATER DROPLETS IN THE POLLINATION OF *PLATANTHERA AQUILONIS* (ORCHIDACEAE)

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ABSTRACT. The North American *Platanthera aquilonis* Sheviak has long been known to autopollinate. Pollinia rotate forward and downward out of the anther sacs and contact the stigma. Previous experimental evidence has indicated that this movement is effected by gravity. In addition to the movement of whole pollinia, flowers are often found in which continuous streams of pollen massulae emanate from anther sacs and seemingly pour down onto the stigma. Experiments with cultivated plants have shown that water droplets can collect in the centers of flowers of this species. These sometimes draw a sheet of massulae out of an anther sac either onto the surface of the droplet or into its interior. As the droplet evaporates, the massulae are deposited as a continuous layer from the anther sac onto the stigma. It is suggested that in nature dew may function to produce the observed pollen streams.

Key Words: *Platanthera aquilonis*, *Platanthera hyperborea*, pollination

The recently described *Platanthera aquilonis* Sheviak is a widespread and well-known North American species that has been confused with the Icelandic *P. hyperborea* (L.) Lindl. (Sheviak 1999). Autogamy in the North American species has long been known, having been reported [as *Habenaria hyperborea* (L.) R. Br.] by Asa Gray (1862a, 1862b). Shortly after the flower opens, or sometimes while still in the bud, the weak caudicle bends and the pollinia are said to fall onto the stigmatic surface below (Gray 1862a, 1862b; Catling 1983; Catling and Catling 1991). Catling (1983) determined that the motion evidently is driven by gravity, as it did not occur in experimentally inverted flowers.

My experience with cultivated plants of *Platanthera aquilonis* largely confirms these earlier findings. In plants from across much of the range of the species, from Alaska to Illinois and New York, a bending of the caudicle rotates the pollinium forward through a longitudinal fissure in the anther sac and downward onto the stigma. This process may be evident in newly opened flowers or may be delayed for several days. A common feature of plants in the field, however, and clearly evident in the herbarium, suggests that an additional process is at work. The pollinia are very loosely organized (again as reported by Gray 1862b), with massulae (i.e., primary groups of pollen tetrads) only weakly bound secondarily into easily fragmented pollinia. Quite commonly, loose massulae emanate from anther sacs still enclosing the remnants of pollinia and trail down onto the stigma. How this condition arises has not previously been reported; evidence suggesting a plausible causative agent is presented here.

MATERIALS AND METHODS

A number of plants of *Platanthera aquilonis* from various sites across the range of the species have been maintained in cultivation for many years. They are grown in a modern office building under a motorized track-mounted 1000-watt metal halide lamp. The area has been used for over 20 years to grow plants of various species of *Platanthera, Spiranthes*, and other genera. Conditions are suitable for maintenance of normal phenotype expression, and many individual plants have survived throughout this period. In 1997 one plant of *P. aquilonis* from Illinois (McHenry Co., *Sheviak 5599*), and in 1999 two plants from New York (Essex Co., *Sheviak 6229*) were employed in experiments. Temperatures were maintained within a few degrees of 20°C, but humidity varied widely.

In 1997 the Illinois plant produced a large inflorescence, and flowers opened over a period exceeding one month in length. Despite this protracted interval, near the end of the period no flowers had been pollinated and all pollinia remained enclosed within the anther sacs. In the several years of cultivation of plants of this species, this was the first case noted in which autopollination had not occurred. The humidity in the growing area at that time was uniformly quite low, so I suspected that the anther sacs might have been unusually rigid, thereby trapping the pollinia. This provided an unusually clear opportunity to investigate the possible role of humidity in pollination, since autopollination was not occurring by any means, and humidity could be readily manipulated.

In the initial trial in 1997, a very fine mist of water from a hand pump atomizer was directed at the inflorescence of the Illinois plant, and the plant was enclosed in a colorless transparent plastic cylinder closed at the top but open at the bottom to permit limited air exchange yet retain humidity. The walls of the cylinder were also sprayed to create a humid chamber. The chamber was removed for the night, and, following some initial positive response that was evident the following morning, the misting was repeated. In 1999 verification was attempted, and the same procedure was repeated on the two New York plants.

RESULTS

With the first misting of the Illinois plant, numerous very small drops of water formed on the floral segments. In many cases these immediately coalesced to form a single large drop that occupied the center of the flower, immersing the column. After 90 minutes the water had evaporated from the flowers. At that time there was no noticeable change in the flowers, but the following morning several pollinia were found to be protruding from the anther sacs; one was nearly completely free of the sac. With the second misting, drops again formed in the centers of the flowers. In several flowers, within 30 minutes of application, the massulae were drawn out onto the surface of the water droplet as if pulled by the surface tension. As the water evaporated, the pollen maintained its position. Eventually, following the complete evaporation of the water, the pollen remained, forming a continuous sheet from the surface of the stigma to the remains of the pollinium within the anther sac.

The New York plants were misted within a few days of the flowers' opening. At that time pollinia were already appearing and a few flowers had been pollinated. The flowers this time proved to be more hydrophobic than in the preceding example, with the result that water tended to drip off of the flowers rather than be drawn into them. Nonetheless, some drops did form in the centers of flowers. The results in these cases were somewhat

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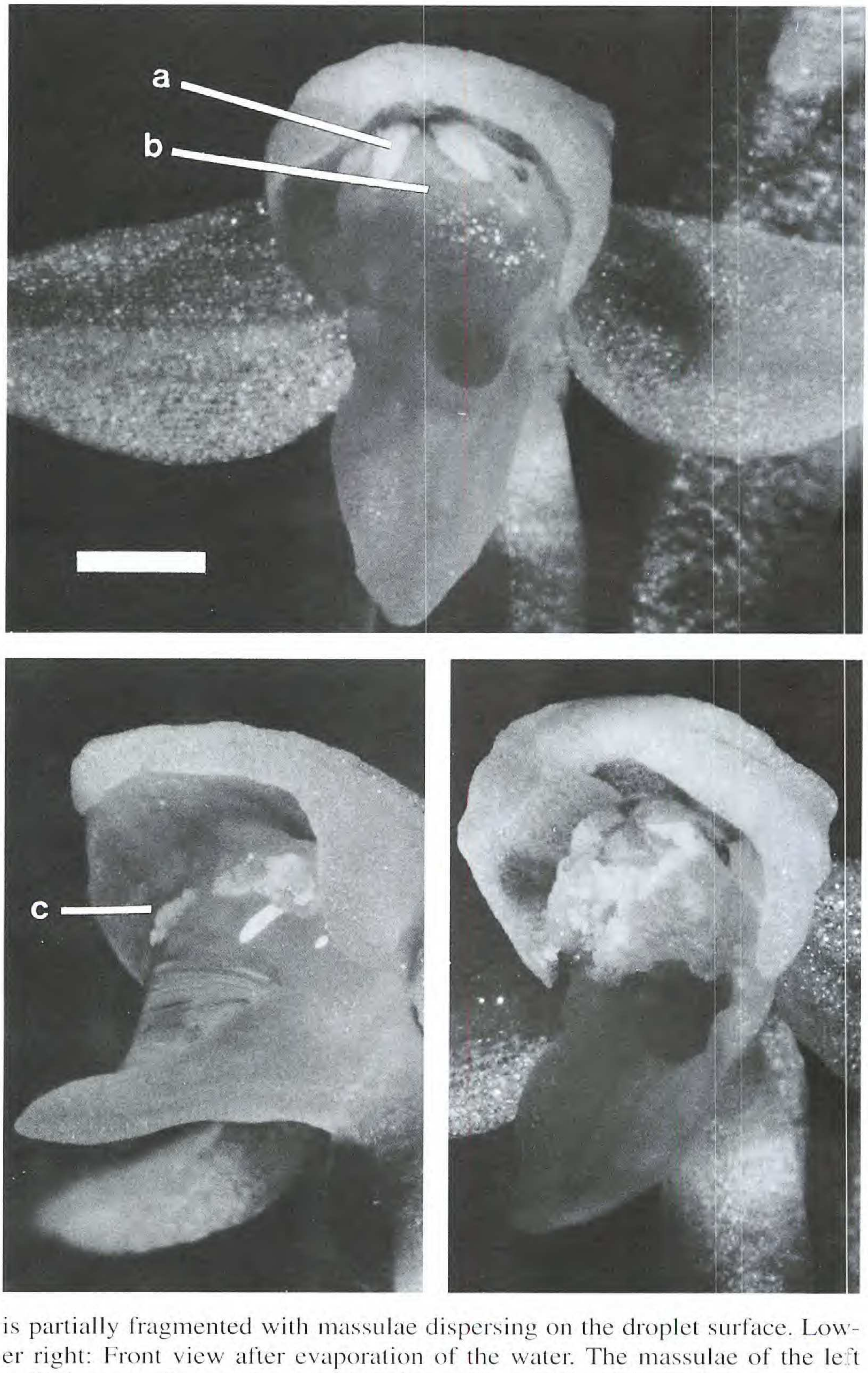
Figure 1. One of the flowers of *Platanthera aquilonis* from New York showing autopollination effected by a central water droplet. All to same scale; scale bar = 1 mm. Top: Front view before treatment. Pollinia (white bodies) are fully exposed within the open anther sacs; a – pollinium (one of two); b – stigma. Lower left: Oblique view showing central water droplet (note arching reflections on surface of droplet). c – Pollinium on the left is free of the anther sac and is riding on the surface of the droplet; pollinium on the right



is partially fragmented with massulae dispersing on the droplet surface. Lower right: Front view after evaporation of the water. The massulae of the left pollinium are dispersed across the stigma. Most of the right pollinium remains within the anther sac, but a stream of massulae extends from the sac down across the stigma.

different than in the preceding trial. In most cases whole pollinia were drawn into the drop, or sometimes onto its surface. Only rarely did massulae stream out, and then sometimes this occurred within the drop rather than on its surface. Examples are shown in Figure 1. With the evaporation of the drop, whole pollinia were deposited on the stigma, or in some cases within the mouth of the spur or even on a floral segment. In those few cases where separated massulae emanated from the anther sac, a sheet of pollen was deposited across the stigma. The massulae in these plants appeared more tightly bound together than in the Illinois plant, with the result that the pollen was not deposited so evenly as in that case.

DISCUSSION

These results bring to mind the cases of *Liparis loeselii* (L.) L. C. Rich., a common associate of *Platanthera aquilonis*, and the tropical *Oeceoclades maculata* (Lindl.) Lindl. In these species, however, the actual impact of raindrops has been implicated in pollination. In *Liparis*, the drops have been found to physically dislodge partially exposed pollinia (Catling 1980), and in *O. maculata*, the impact apparently removes the anther cap and permits the pollinia to hang near the stigma, where another, undetermined agent effects actual pollination (González-Díaz and Ackerman 1988).

The very limited trials reported here indicate a plausible origin for the pollen streams that had previously been noted on *Platanthera aquilonis* flowers in the field and herbarium. Additionally, these trials account for the placement of pollinia on perianth surfaces and within spurs, as has also sometimes been seen. In *P. aquilonis* any wetting of the inflorescence that leads to formation of droplets in the centers of the flowers may facilitate pollination. The coalescence of very small droplets into larger central ones that was seen in the present experiments suggests that dew might commonly function in this capacity. Rain might also in some cases be effective, but it was not simulated during this study; the hooded perianth and its rather hydrophobic surfaces may tend to deflect raindrops. Less common meteorological conditions, such as blowing fog or mist, might function similarly to dew, but they would not be expected to be significant except in certain areas where they were common phenomena.

The frequency of suitable droplet formation would be expected to vary with the habitat, and the relative influence of gravity- and water-assisted pollination may vary accordingly. Certainly the latter is lacking unless water is present, but it may be important in areas with frequent dew formation during anthesis. Furthermore, partially offsetting the positive effects of droplet formation is pollen loss through deposition in spurs and on perianth surfaces. Hence, in areas where dew is frequent during anthesis, incoherent pollinia might represent part of a water pollination syndrome subject to selection through increased pollination and reduced loss of pollinia. In this regard, it may be significant that the Illinois plant, with its very loosely associated massulae, was from an open wet prairie where dew formation was likely a common occurrence. In contrast, the New York plants were found in a dense forest of *Tsuga canadensis* Carrière with *Acer saccharum* Marshall on a rather dry hillside; in such a situation dew formation is probably an uncommon occurrence, and the less fragile pollinia of these plants may reflect a prevalence in this population of gravity-assisted rotation and a rarity of water pollination.

This speculation on possible evolutionary significance of these observations is based on a very small sample and obviously a larger and geographically more diverse sample is necessary for verification. Further study of this novel pollination mechanism, especially in natural populations occurring under diverse conditions, might prove valuable. In addition to gravity- and water-assisted autopollination, the flowers retain the structures necessary for insect pollination, thus suggesting a third dimension that might be important in some situations. *Platanthera aquilonis* thus may be a significant subject for study of the evolution of pollination mechanisms.

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LITERATURE CITED

CATLING, P. M. 1980. Rain-assisted autogamy in *Liparis loeselii* (L.) L. C. Rich. (Orchidaceae). Bull. Torrey Bot. Club 107: 525–529.

———. 1983. Autogamy in eastern Canadian Orchidaceae; a review of current knowledge and some new observations. Naturaliste Canad. 110: 37–53.

——— and V. R. Catling. 1991. A synopsis of breeding systems and pollination in North American Orchids. Lindleyana 6: 187–210.

González-Díaz, N. and J. D. Ackerman. 1988. Pollination, fruit set, and seed production in the orchid, *Oeceoclades maculata*. Lindleyana 3: 150–155.

Gray, A. 1862a. Enumeration of the plants of Dr. Parry's collection in the Rocky Mountains. Amer. J. Sci. Arts, Ser. 2. 34: 249–261.

———. 1862b. Fertilization of Orchids through the agency of insects. Amer. J. Sci. Arts, Ser. 2. 34: 420–429.

Sheviak, C. J. 1999. The identities of *Platanthera hyperborea* and *P. huronensis*, with the description of a new species from North America. Lindleyana 14: 193–203.